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Maas, H.; Huijing, P.A.J.B.M.

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ORIGINAL ARTICLE

Huub Maas · Peter A. Huijing

Myofascial force transmission in dynamic muscle conditions: effects of dynamic shortening of a single head of multi-tendoned rat extensor digitorum longus muscle

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Abstract This study investigated the effects of myofascial force transmission during dynamic shortening of head III of rat extensor digitorum longus muscle (EDL III). The anterior crural compartment was left intact. Force was measured simultaneously at the distal EDL III tendon, the proximal EDL tendon and the distal tendons of tibialis anterior and extensor hallucis longus muscles (TA + EHL). Two types of distal shortening of EDL III were studied: (1) sinusoidal shortening (2 mm) and (2) isokinetic shortening (8 mm). Sinusoidal shortening of EDL III caused a decrease in force exerted at the distal tendon of EDL III: from 0.58 (0.08) N to 0.26 (0.04) N. In contrast, hardly any changes in proximal EDL force and distal TA + EHL force were found. Maximal concentric force exerted at the distal tendon of EDL III was higher than maximal isometric force expected on the basis of the physiological cross-sectional area of EDL III muscle fibers (Maas et al. 2003). Therefore, a substantial fraction of this force must originate from sources other than muscle fibers of EDL III. Isokinetic shortening of EDL III caused high changes in EDL III force from 0.97 (0.15) N to zero. In contrast, changes in proximal EDL force were much smaller: from 2.44 (0.25) N to 1.99 (0.19) N. No effects on TA + EHL force could be shown. These results are explained in terms of force transmission between the muscle belly of EDL III and adjacent tissues. Thus, also in dynamic muscle conditions, muscle fiber force is transmitted via myofascial pathways.

Keywords Connective tissue · Multi-tendoned muscle · Concentric contractions · Myofascial force transmission · Repetitive strain injury

H. Maas
School of Applied Physiology, Georgia Institute of Technology, 281 Ferst Drive, Atlanta, GA 30332-0356, USA
E-mail: huub.endemaas@ap.gatech.edu

H. Maas · P. A. Huijing (✉)
Instituut voor Fundamentele en Klinische Bewegingswetenschappen, Faculteit Bewegingswetenschappen, Vrije Universiteit, van der Boechorststraat 9, 1081 BT, Amsterdam, The Netherlands
E-mail: p_a_j_b_m_huijing@fbw.vu.nl
Tel.: +31-20-4448476
Fax: +31-20-4448529

P. A. Huijing
Integrated Biomedical Engineering for Restoration of Human Function, Instituut voor Biomedische Technologie, Faculteit Constructieve Technische Wetenschappen, Universiteit Twente, Enschede, The Netherlands

Introduction

Several human tasks, such as typing on a keyboard and playing a musical instrument require movements of fingers relative to each other. In general, multi-tendoned muscles of the forearm contribute to finger flexion and extension. Movements of fingers relative to each other involve muscle–tendon complex length changes of the corresponding muscle heads. Consequently, some heads of a multi-tendoned muscle may be active at high length, while simultaneously other heads are active at a lower length. In such conditions, the position of muscle heads relative to each other changes, as well as their position relative to other surrounding muscular and non-muscular structures.

For rat whole extensor digitorum longus muscle (EDL) within an intact anterior crural compartment, it has been shown recently that muscle relative position is a co-determinant of isometric muscle force (Huijing and Baan 2003; Maas et al. 2004, 2003b, c). Such position effects have been explained in terms of force transmission out of the muscle via pathways other than the tendons, i.e. inter- and extramuscular myofascial force transmission (Huijing and Baan 2001a; Maas et al. 2001). Previous studies (Huijing et al. 1998; Jaspers et al. 2002) on fully dissected multi-tendoned rat EDL muscle yielded clear evidence of transmission of force between muscle heads via connective tissue at their interface (i.e. intramuscular myofascial force transmission). Recently, force transmission between a single head of EDL muscle

and adjacent synergists as well as extramuscular structures was found (Maas et al. 2003a).

All previous experiments on myofascial force transmission involved isometric muscle contractions exclusively. Therefore, in the present work, effects of two types of dynamic shortening of one head of rat EDL muscle (head III, referred to as EDL III) were studied (i.e. small sinusoidal and long-range isokinetic shortening). The first purpose of this study was to test the hypothesis that also in dynamic muscle conditions force is transmitted between EDL III and adjacent tissues via intramuscular myofascial pathways, as well as via inter- and extramuscular myofascial pathways. The second purpose was to compare the effects of myofascial force transmission in isometric and dynamic muscle conditions.

Methods

Surgical and experimental procedures were in strict agreement with the "Principles of laboratory animal care" (NIH Pub. 86–23, revised 1985) as well as the guidelines and regulations concerning animal welfare and experimentation set forth by Dutch law, and approved by the Committee on Animal Experimentation at the Vrije Universiteit.

Surgical procedures

Male Wistar rats ($n = 11$, body mass = 310.7 g, SD 25.2) were anaesthetized by intraperitoneal injection of a 12.5% urethane solution (1.2 ml·100 g^{-1} body mass; if necessary, extra doses were given to maintain deep anesthesia: maximally 1.5 ml). To prevent hypothermia during surgery and data collection, the animals were placed on a heated water pad of approximately 37°C. Ambient temperature (22°C, SD 0.5) and air humidity (80%, SD 2) were kept constant by a computer-controlled air-conditioning system. Dehydration of muscle and tendon tissue was prevented by regular irrigation with isotonic saline.

Removing the skin and most of the biceps femoris muscle from the left hind limb exposed the anterior crural compartment, which envelopes the tibialis anterior (TA), extensor digitorum longus (EDL) and extensor hallucis longus (EHL) muscles. Connective tissues of the compartment at the muscle bellies of TA, EHL and EDL as well as the retinaculae at the ankle (i.e. transverse crural ligament and the crural cruciate ligament) were left intact.

Multi-tendoned EDL muscle consists of four heads of which the muscle fibers share a common aponeurosis and tendon proximally, but have individual aponeuroses and tendons distally (Balice-Gordon and Thompson 1988; Maas et al. 2003a). The muscle fibers of head V insert into the most distal portion of the proximal aponeurosis, the muscle fibers of head III and IV proximal to that, and the muscle fibers of head II insert into the most proximal portion of the proximal aponeurosis (for an image see Fig. 2 Maas et al. 2003a).

The heads are named after their insertions on the digits of the foot (II, III, IV and V). In the foot, the distal tendon of head III of EDL muscle (EDL III) as well as the distal tendons of TA and EHL muscles were dissected free from surrounding tissues. As EDL III is directly connected to head II and IV of EDL muscle as well as to the muscle belly of TA (Maas et al. 2003a), this muscle head was selected. The distal tendons of TA and EHL muscles are, for a substantial part of their length, quite close to one another. As it is difficult to measure force exerted at each tendon individually without friction between them, the distal tendons of TA and EHL were tied together using polyester thread (further referred to as TA + EHL), with the ankle joint at 90° (Fig. 1). The distal tendon of EDL III and the distal tendons of the TA + EHL complex were cut and Kevlar threads (diameter = 0.5 mm, tensile modulus = 58 GPa, 3.7% extension to breaking; Goodfellow, Cambridge, England) were tied to them. The foot was attached to a plastic plate with tie wraps. The femoral compartment was opened in order to (1) cut a small piece of the lateral epicondyle of the femur (i.e. the origin of EDL muscle) for attaching it to Kevlar thread, (2) to secure a metal clamp to the femur for later fixation at a knee angle of 100° in the experimental apparatus, and (3) to dissect the sciatic nerve.

Within the femoral compartment, the sciatic nerve branches into the tibial nerve, the sural branch and the common peroneal nerve. The common peroneal nerve enters the anterior crural compartment from the

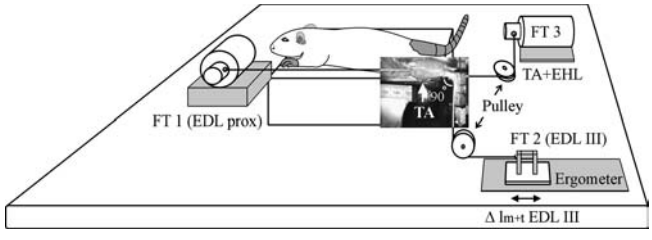

Fig. 1 A schematic representation of the experimental set-up. A lateral view of the lower leg of the rat left hind limb in the experimental set-up is shown. As EDL and EHL muscles are enclosed by TA muscle, only the latter muscle is visible. *FT1* indicates the force transducer connected to the proximal tendon of EDL muscle, *FT2* indicates the force transducer mounted on a multipurpose muscle ergometer connected to the distal tendon of EDL III, *FT3* indicates the force transducer connected to the distal tendons of TA and EHL muscles. Kevlar thread was used to connect the muscles to force transducers. A low friction pulley guided the Kevlar thread from TA + EHL to FT3 that, for reasons of space, was placed perpendicular to the other force transducers. The proximal tendon of EDL muscle was connected directly to the force transducer, which was positioned in the line of pull. The distal tendon of EDL III was connected to the force transducer via a low friction pulley. Various muscle–tendon complex lengths of EDL III were obtained by repositioning the ergometer (i.e. FT2), as indicated by the *double arrow*

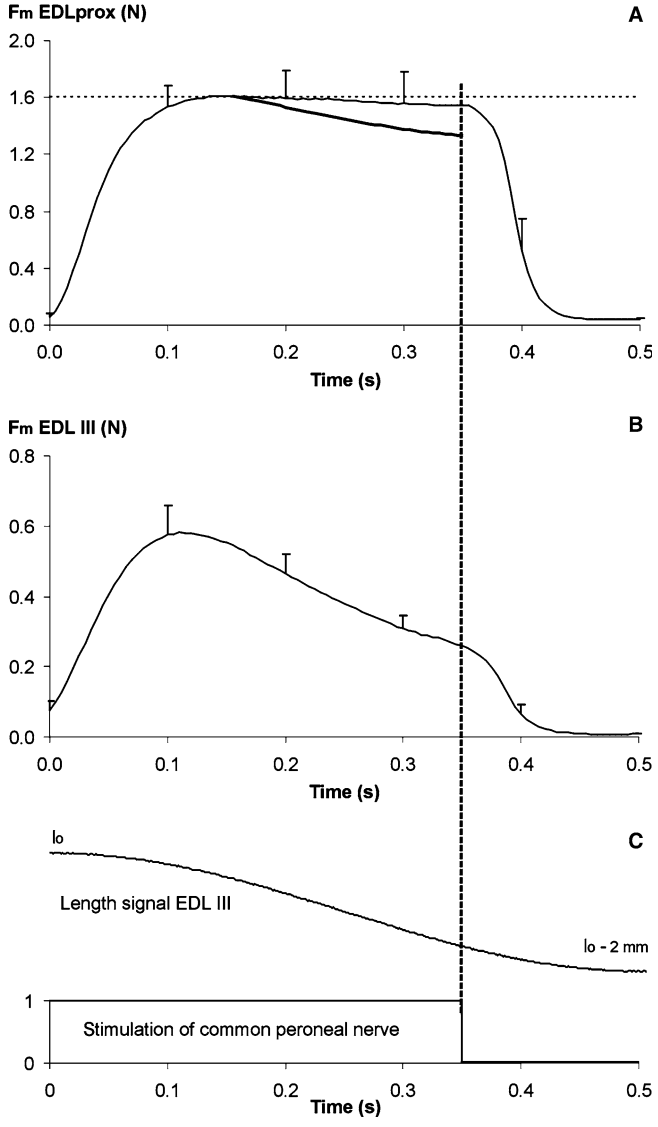

Fig. 2 EDL total forces during sinusoidal concentric length changes of EDL III. **a** Mean of traces of total force (F_m) exerted in time at the proximal tendon of EDL. Proximal EDL force if its changes would be equal to changes of EDL III force (see **b**) were calculated. For the time period between occurrence of maximal force and the end of stimulation, this calculated force is superimposed. **b** Mean traces of total force (F_m) exerted at the distal tendon of EDL III. **c** EDL III length and stimulation of the common peroneal nerve. Passive EDL III was brought to high length (*lo*). Subsequently, stimulation of the nerve and shortening (from *lo* to *lo*-2 mm) of EDL III were started simultaneously. Muscles are excited maximally for 0.35 s. Note that the active shortening of EDL III follows a sinusoidal trajectory in time. Stimulation of the common peroneal nerve causes activation of EDL, TA and EHL muscles as well as the muscles in the peroneal compartment. The end of nerve stimulation is indicated (*vertical dotted line*). The *horizontal dotted line* in **a** indicates maximal force of proximal EDL. Values are shown as mean (SD), $n = 5$

peroneal compartment through a fenestration within the anterior intermuscular septum (Huijing and Baan 2001b, 2003). Branches of the intact common peroneal nerve innervate EDL, TA and EHL muscles as well as the muscles in the peroneal compartment. The tibial nerve, the sural branch as well as all other more proximal branches of the sciatic nerve were cut. As cutting the branches of the common peroneal nerve innervating the peroneal muscles would involve opening of the anterior crural compartment and further dissection, denervation of these muscles was not performed. The sciatic nerve, with only the common peroneal nerve branch left intact, was dissected and cut as proximally as possible.

Mounting the animal in the experimental apparatus

The rat was placed on a platform. The metal clamp was used to secure the femur at a knee angle of 100° (Fig. 1). The plastic footplate was positioned in such a way that the ankle angle was 90°. Using the Kevlar threads, the proximal tendon of EDL muscle as well as the distal tendons of TA + EHL were connected to force transducers (maximal output error < 0.1%, compliance of 0.0048 mm/N; Hottinger Baldwin, Darmstadt, Germany) mounted on single axis micropositioners, and the distal tendon of EDL III was connected to a force transducer (compliance 0.014 mm/N) mounted on a multipurpose muscle ergometer (Woittiez et al. 1987). The other distal tendons of EDL muscle were left attached to their insertions on the digits within the foot (i.e. II, IV and V). For TA + EHL force measurements, the Kevlar thread was connected to the force transducer via a low friction pulley that, for reasons of space, was placed perpendicular to the other force transducers. For EDL head III distally, a natural pulley (i.e. the retinaculae at the ankle) causes its line of pull to be in parallel with the foot. To connect the Kevlar thread to the force transducer on the ergometer, an additional pulley was needed. The proximal tendon of EDL muscle was connected directly to the force transducer, which was positioned in the line of pull.

In order to make sure that the pulleys introduced no artifact, a possible force leak due to friction of the pulley was assessed. Calibrated weights were connected to a force transducer via the pulley using a Kevlar thread. Subsequently, the pulley was moved with a constant velocity and force exerted at the Kevlar thread was measured. The difference between the measured force and the applied weight was maximally 0.2%.

The sciatic nerve, with only the common peroneal nerve branch left intact, was placed in a pair of silver electrodes. The nerve was prevented from dehydration, by covering it with paper tissue saturated with isotonic saline covered by a thin piece of latex. In all experimental conditions, the sciatic nerve was stimulated supramaximally using electrodes connected to a constant current source (3 mA, pulse width 100 μs, frequency 100 Hz). Nerve stimulation activated EDL, TA, EHL muscles as well as the muscles in the peroneal compartment simultaneously. The peroneal muscles are located in a separate compartment and were kept at a constant muscle–tendon complex length as well as a constant relative position (constant ankle joint angle, see

below). Therefore, any effects of activation of these antagonistic muscles (not measured in the present experiment) were expected to be constant for all experimental conditions tested.

Experimental protocols

For all experimental conditions, TA + EHL muscle–tendon complex length (corresponding to an ankle joint at 90°) was kept constant. This was also the case for the position of the proximal tendon of EDL muscle (corresponding to a knee joint at 100°). In addition, the distal tendons of EDL head II, IV, and V were left attached to their insertions. Therefore, their muscle–tendon complex lengths were also kept constant. In this way, effects of changes of length and relative muscle position of these muscles on force transmission from EDL III (Huijing and Baan 2003; Maas et al. 2001, 2004) were excluded.

In the experiment, EDL III was allowed to shorten dynamically, leading to changes of its muscle–tendon complex length, as well as to changes of its position relative to (1) other EDL heads, (2) adjacent muscles and (3) extramuscular tissues. Time traces of force exerted at the distal tendon of EDL III, the proximal EDL tendon and the distal tendons of the TA + EHL complex, were collected using a 12-bit A/D converter (sampling frequency 1,000 Hz, resolution of force <0.01 N, resolution of length <2.5 μm). Timing of stimulation of the nerve, length changes of EDL III and A/D conversion were controlled by a special-purpose microcomputer.

Before acquiring data, EDL muscle was preconditioned by isometric contractions at several high lengths of EDL III until isometric forces at low and high EDL III length were reproducible (Maas et al. 2003a). Subsequently, isometric optimum length (*l*o) of EDL III was determined at the distal tendon using procedures described previously (Maas et al. 2003a). Isometric force was measured at various lengths of EDL III. EDL III was lengthened at its distal tendon with 1 mm increments starting at active slack length (i.e. the lowest length at which active force approaches zero) until approximately 2 mm over optimum length. The length at which active force exerted at the distal tendon of EDL III was maximal is defined as optimum length.

Two types of concentric contractions of EDL III were imposed: a) *Sinusoidal shortening of EDL III* ($n=5$). Passive EDL III was lengthened distally to isometric optimum length. Subsequently, stimulation of the common peroneal nerve and shortening of EDL III were started simultaneously. EDL III was allowed to shorten over a limited length range (i.e. from lo to *l*o–2 mm in 0.5 s). To make sure that the muscles were fully relaxed by the end of shortening, nerve stimulation was turned off after 0.35 s (Fig. 2c). Note that active shortening of EDL III follows a sinusoidal trajectory in time, i.e. length and shortening velocity change in time according to sinusoidal curves (maximal velocity = 6.28 mm·s^{-1}). b) *Isokinetic shortening of EDL III* ($n=6$). Before each contraction, passive EDL III was brought to the desired length (*l*o + 1 mm) by moving the ergometer force transducer (Fig. 4c). Subsequently, the common peroneal nerve was stimulated without any changes of EDL III length, to allow building up of isometric force (pulse train 300 ms). While muscle stimulation continued (pulse train 1,600 ms), EDL III was shortened isokinetically by 8 mm (i.e. from *l*o + 1 mm to lo−7 mm, velocity = 5 mm s^{-1}).

Treatment of force data and statistics

For all force data, means and standard deviations (SD) were calculated. Although forces exerted at the distal tendons of EDL III and the TA + EHL complex are in opposite direction to forces exerted at the proximal tendon of EDL, all forces will be presented as positive values.

To test for effects of EDL III muscle–tendon complex length on proximal EDL force, distal EDL III force and TA + EHL complex force, one-way ANOVA's for repeated measures were performed. P values <0.05 were considered statistically significant.

Results

Effects of small concentric length changes of EDL III

In Fig. 2, mean traces of total force exerted at the distal tendon of EDL III and at the proximal tendon of whole EDL during small concentric length changes of EDL III are shown.

EDL proximal force (Fig. 2a)

At $t=0$ s, a small passive force of 0.06 (0.02) N was exerted at the proximal tendon. After concurrent simultaneous onset of stimulation of the common peroneal nerve (exciting EDL, TA and EHL muscles) and the start of EDL III shortening, proximal EDL force built up to a maximum of 1.61 (0.19) N. Despite the fact that the shortening muscle fibers of head III have the capability to transmit force onto the proximal aponeurosis of EDL, the proximal EDL force trace resembles that of an isometric contraction. After reaching a plateau, force exerted at the proximal tendon of EDL remained fairly constant (it decreased by only 0.07 N, i.e. by 4.3%) and no very obvious effects of progressive shortening of EDL III are observed. After nerve stimulation was switched off, proximal EDL force dropped to 0.04 (0.01) N. These results indicate that small dynamic length changes of EDL III hardly affect proximal EDL force.

Distal EDL III force (Fig. 2b)

Since EDL III was brought to optimum length (*l*o) prior to excitation of the muscles, some passive force (0.08 N, SD 0.03) was exerted at the starting time of stimulation

($t = 0$ s). After the simultaneous onset of nerve stimulation and EDL III shortening, EDL III force built up to a maximum of 0.58 (0.08) N. Due to the fact that the length signal follows a sinusoidal curve, EDL III was shortened by only 0.23 mm at the time maximal force was measured ($t = 0.11$ s). Until stimulation was switched off ($t = 0.35$ s), a further decrement of EDL III muscle–tendon complex length ($\Delta lm + t = 1.36$ mm) caused EDL III force to decrease progressively: to 0.26 (0.04) N, i.e. by 55%. After stimulation of the common peroneal nerve was switched off, EDL III total force decreased to near zero (i.e. passive force exerted at its new length, $lo-2$ mm, was smaller than 0.01 N).

If all force generated within the muscle fibers of EDL III would be transmitted exclusively onto the proximal EDL tendon, changes of force exerted at the proximal tendon of EDL are comparable to the changes of force exerted at the distal tendon of EDL III. Figure 2 clearly shows that this was not the case. For mechanical equilibrium, the sum of the forces exerted proximally should equal the sum of the forces exerted distally. Therefore, it is concluded that force is transmitted via myofascial pathways between EDL III and its surrounding muscular and/or non-muscular structures.

TA + EHL complex force (Fig. 3)

Mean traces of total force exerted at the distal tendons of the TA + EHL complex during small dynamic length changes of EDL III are shown. Passive TA + EHL force exerted at $t = 0$ s was very small: 0.01 (0.03) N. After an initial steep rise, distal TA + EHL force remained almost constant. Passive TA + EHL force exerted at the end of EDL III shortening, i.e. 0.04 (0.04) N, was slightly increased, but not significantly different from passive force prior to EDL III shortening. These results indicate no net intermuscular myofascial force transmission between EDL III and TA + EHL during small dynamic length changes of EDL III.

Effects of isokinetic shortening of EDL III

To assess if the limited effects of dynamic shortening of EDL III on proximal EDL force and distal TA + EHL force can be ascribed to the limited length range, EDL III was shortened isokinetically (velocity = 5 mm s^{-1}) over a larger length range (i.e. by 8 mm) (Fig.4c). Mean traces of total force exerted at the distal tendon of EDL III and the proximal tendon of whole EDL are shown in Fig. 4.

EDL proximal force (Fig. 4a)

Before EDL III was shortened, a small passive force of 0.06 (0.04) N was exerted at the proximal EDL tendon. After building up of isometric force, active shortening of EDL III imposed via its distal tendon decreased

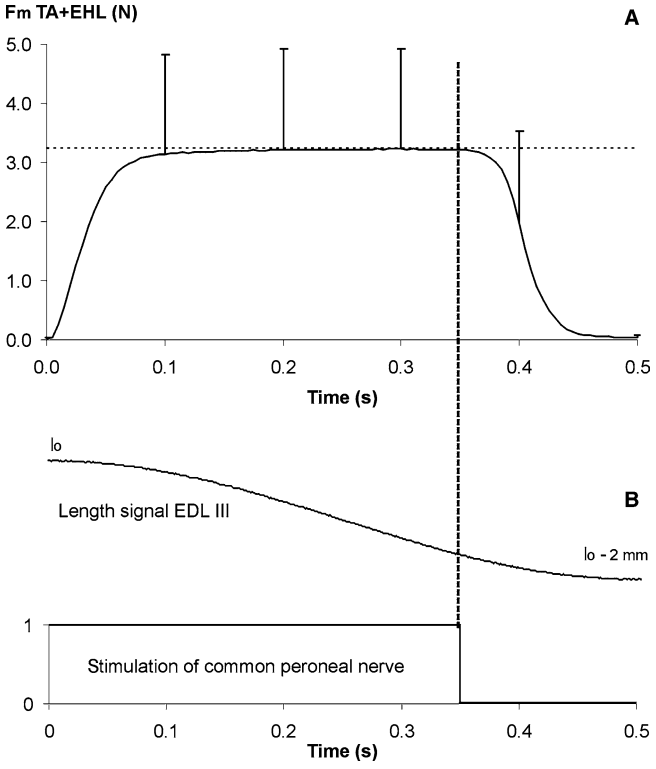

Fig. 3 Total force of TA + EHL during small concentric length changes of EDL III. **a** Mean traces of total force (F_m) exerted at the distal tendons of TA + EHL. **b** EDL III length and stimulation of the common peroneal nerve (see legend Fig. 2). The end of nerve stimulation is indicated (*vertical dotted line*). The *horizontal dotted line* indicates maximal total force of the TA + EHL complex. Values are shown as mean (SD), $n = 5$

proximal EDL total force exponentially from 2.44 (0.25) N to 1.99 (0.19) N, i.e. by 18%. After full relaxation of EDL muscle, proximal passive force was zero.

Distal EDL III force (Fig. 4b)

As EDL III was kept initially at over isometric optimum length ($lo + 1$ mm), a substantial passive force was exerted at the distal tendon of EDL III: 0.13 (0.03) N. After building up of isometric force, distal total force of EDL III decreased exponentially from 0.97 (0.15) N to zero, due to shortening velocity and length effects. After full relaxation of EDL muscle, distal passive force was zero.

These results show that even with substantial dynamic length changes of EDL III, force changes at the distal tendon of EDL III are not equal to force changes at the proximal EDL tendon: changes of EDL III distal force were approximately twice the changes of proximal EDL force. Therefore, it seems likely that during more extreme shortening similar mechanisms are active as during small sinusoidal length changes.

TA + EHL complex force (Fig. 5)

Initial passive force exerted by the TA + EHL complex, kept at a constant moderate length, was negligible. After

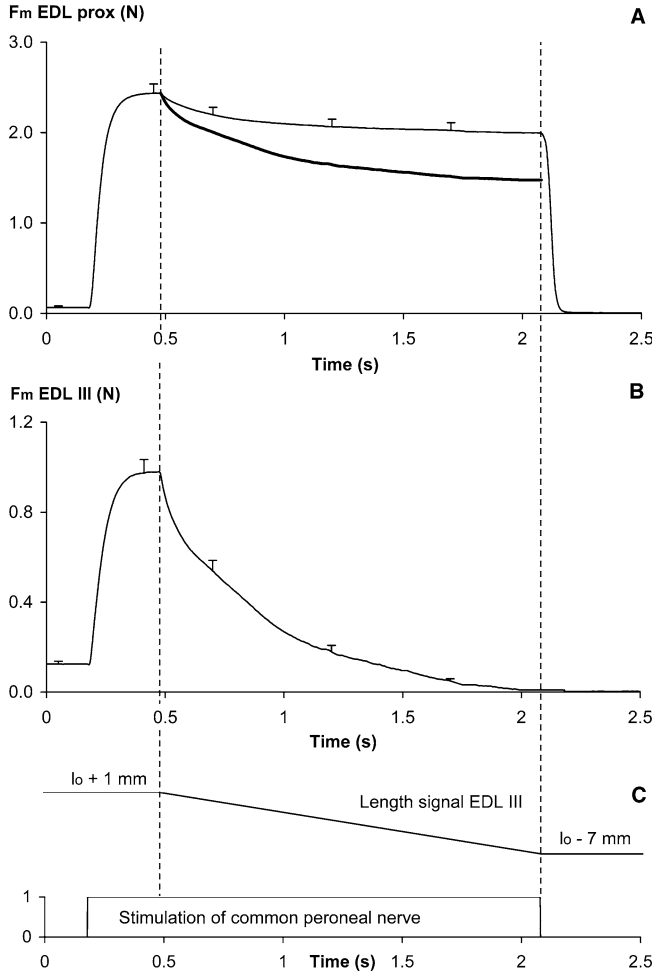

Fig. 4 EDL total forces during long range isokinetic shortening of EDL III. **a** Mean traces of total force (F_m) exerted at the proximal tendon of EDL. Proximal EDL force if its changes would be equal to changes of EDL III force (see **b**) were calculated. For the time period between occurrence of maximal force and the end of stimulation, this calculated force is superimposed. **b** Mean traces of total force (F_m) exerted at the distal tendon of EDL III. **c** EDL III length and stimulation of the common peroneal nerve. After building up of isometric force, EDL III was shortened isokinetically (velocity = 5 mm/s) by 8 mm (i.e. from *lo* + *1* mm to *lo*-7 mm). The start and end of EDL III shortening is indicated (*vertical dotted lines*). Values are shown as mean (SD), $n = 6$

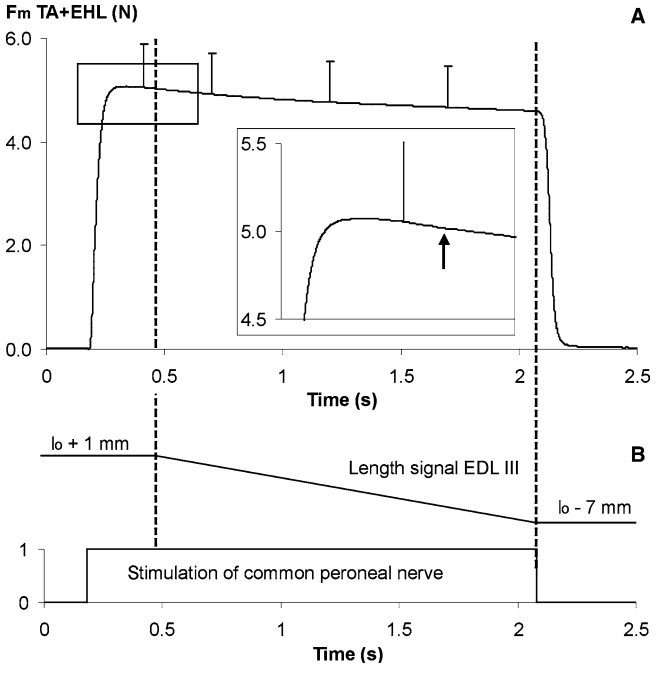

Fig. 5 Total force of TA + EHL during long range isokinetic shortening off EDL III. **a** Mean traces of total force (F_m) exerted at the distal tendons of TA + EHL. Note that the time–force signal is not perturbed by the onset of isokinetic shortening of EDL III as shown by the magnification of the time–force trace (see inset, *the arrow* indicates the start of EDL III shortening). **b** EDL III length and stimulation of the common peroneal nerve (see legend Fig. 4). The start and end of EDL III shortening is indicated (*vertical dotted lines*). Values are shown as mean (SD), $n = 6$

building up of isometric force, mean total TA + EHL force decreased monotonically during the tetanic contraction of these muscles from 5.07 (0.83) N to 4.60 (0.76) N, i.e. by 9.3%. It should be noted that the time-force signal of TA + EHL is not perturbed by the onset ($t = 0.48$ s) of isokinetic shortening of EDL III (i.e. see magnification of time–force signal). These results constitute no unequivocal evidence for intermuscular interactions between EDL III and the TA + EHL complex during dynamic EDL III shortening. As the muscles are activated for 1,900 ms, the decrement of TA + EHL force in time may be well explained by other effects, such as fatigue due to sustained maximal excitation of TA and EHL muscles (Willems and Stauber 1999).

Discussion

To the best of our knowledge, this is the first systematic study regarding effects of myofascial force transmission during controlled dynamic changes of muscle–tendon complex length. The major result of the present study is that changes of force exerted at the proximal tendon of whole EDL muscle as a result of dynamic shortening of head III of EDL muscle were substantially different from changes of distal EDL III force. No effects of such EDL III length changes on force exerted at the distal tendons of TA and EHL muscles were found. Therefore, these results are explained in terms of myofascial force transmission between EDL III and surrounding heads (i.e. intramuscular) as well as non-muscular surrounding structures (i.e. extramuscular).

Our present experiments yielded more evidence for such a conclusion. Recently, it was reported that the mass of head III of EDL muscle expressed as a percentage of total EDL muscle mass was 16 (2.2)% (Maas et al. 2003a). As the number of sarcomeres in series within fibers of different EDL heads has been shown to be rather similar (Huijing et al. 1998), values of normalized mass were considered as adequate estimates of normalized physiological cross-sectional area and, thus, of maximal relative contribution of individual heads to total EDL muscle force. In a previous study, optimal

isometric force for whole EDL muscle of rats with similar body mass was 2.60 (0.40) N (Maas et al. 2001). If a comparable optimal EDL force is assumed for the present study, maximal isometric force exerted by the muscle fibers of EDL III onto its distal tendon should be ~0.42 N.

In isometric as well as concentric muscle conditions of the present study, force exerted at the distal tendon of EDL III was higher than this estimated maximal value. Isometric force prior to isokinetic shortening was 0.97 (0.15) N (Fig. 4b). Note that according to the force–velocity characteristics (Hill 1938), maximal force exerted by the muscle fibers of EDL III during concentric contractions should be decreased compared to maximal isometric force. Nevertheless, concentric forces exerted at the distal tendon of EDL III were also higher than maximal isometric force expected on the basis of the physiological cross-sectional area of EDL III muscle fibers: (1) force in the first phase of isokinetic shortening (between $t = 0.48$ s and $t = 0.82$ s, Fig. 4b) and (2) maximal force during sinusoidal shortening, i.e. 0.58 (0.08) N (Fig. 2b)

It is concluded that, also for concentric muscle conditions, a substantial fraction of active force exerted at the distal tendon of EDL III originated from sources other than from muscle fibers of head III.

Non-myofascial mechanical interactions within a muscle–tendon complex

Mechanical interaction between parts of the same muscle has also been investigated by measuring nonlinear summation of force. This is defined (Sandercock 2000) as the difference between the force exerted when both muscle parts are excited simultaneously and the sum of the forces exerted when each muscle part is excited individually. Such a difference as found for isolated cat soleus muscle was explained using a simplified muscle–tendon model with independent fibers connected to a common elasticity (their Fig. 1), which could account for most of the nonlinear summation of force (Sandercock 2000). This model incorporates exclusively mechanical interaction between muscle parts that may occur via a common series elasticity. Note that their conclusions, even though based on a similarity between the experimental results and the model, cannot exclude force transmission between muscle fibers at their interface (i.e. intramuscular myofascial force transmission).

With regard to the present experiment, different heads of EDL muscle are proximally connected to a common aponeurosis and tendon. If each muscle head is considered as fully independent, an increase of force exerted by muscle fibers of one head causes an increase of the length of the proximal aponeurosis and tendon (Ettema and Huijing 1989). This will affect the length and velocity of muscle fibers within adjacent muscle heads of EDL and, consequently, the force exerted by these muscle heads. In the present work, forces exerted at the distal tendons of head II, IV and V of EDL muscle were not measured. As proximal force of isolated EDL muscle is the sum of the forces exerted by the fibers of each muscle head, unequal changes of proximal EDL and EDL III force can, in theory, be the result of such mechanical interaction via a common elasticity.

However, mechanical interaction via a common elasticity cannot explain the result of the present study that force exerted at the distal tendon of EDL III during shortening was substantially higher than the estimated maximal isometric value. Furthermore, previous studies have clearly shown that the muscle heads of rat EDL muscle are linked mechanically to each other (Huijing et al. 1998; Jaspers et al. 2002). Therefore, it is more likely that the difference in force changes between distal EDL III and proximal whole EDL are caused by (1) an altered partitioning of force over the different pathways of force transmission. As EDL III is lengthened, force previously exerted at the distal tendons of head II–IV–V of EDL muscle is exerted at the distal tendon of EDL III; and/or (2) some force exerted at the distal tendon of EDL III is not exerted at the proximal EDL tendon, but is transmitted from the muscle via extramuscular connective tissue directly onto bone.

Intermuscular myofascial force transmission in dynamic muscle conditions

Recently, effects of length of a single head of rat EDL muscle on isometric muscle forces were studied (Maas et al. 2003a). Comparable to the present results (Fig. 4), we found that increasing the length of EDL III distally causes relatively high changes of force exerted at the distal tendon of EDL III, but only limited changes of proximal EDL force. Furthermore, a substantial decrease of EDL III length (i.e. by 9 mm) caused a significant but small increase of isometric TA + EHL force: 0.17 (0.07) N, i.e. 3.4%. In contrast, no unequivocal evidence for intermuscular interactions between EDL III and TA + EHL was found in the present study (Figs. 3, 5). The main difference between these experiments is the condition of EDL III: isometric versus concentric. Therefore, the lack of intermuscular interactions should be explained by effects of dynamic length changes of EDL III. Potential explanations are:

1. Due to effects of shortening velocity of muscle fibers of EDL III, force exerted at its distal tendon is lower compared to isometric force at the same muscle–tendon complex length. If force is decreased the tendon will shorten. As a consequence, fiber length is increased at any muscle–tendon complex length of EDL III. This indicates that changes of the position of the muscle belly of EDL III relative to adjacent synergists are smaller, which may decrease the effects of intermuscular myofascial force transmission. As substantial changes of the relative position of EDL

muscle are still expected, this cannot fully explain the absence of intermuscular interactions.
2. Dynamic shear at the interface between the muscle belly of EDL III and adjacent tissues may decrease the shear stiffness of the structures responsible for intermuscular myofascial force transmission. Such thixotropic effects would decrease the amount of force transmitted via intermuscular myofascial pathways. However, the precise static and dynamic mechanical properties of structures representing myofascial pathways are unknown. Therefore, further experiments are needed to elucidate the mechanisms responsible for the different intermuscular interactions between isometric and concentric muscle conditions.

Implications of myofascial force transmission for the development of muscle disorders in the forearm

Various pathophysiological mechanisms of upper extremity muscle pain have been hypothesized, both at the levels of the peripheral and the central nervous system (for reviews see Armstrong et al. 1993; Forde et al. 2002; Visser and Dieën 2004). Based on experiments in rat muscle compartments, it has been postulated that myofascial force transmission plays a role in the etiology of muscle disorders in the forearm related to repeated movements of fingers relative to each other (Huijing and Baan 2001; Jaspers et al. 2002; Maas et al. 2003).

Movements of fingers relative to each other require shortening of one or more heads of multi-tendoned extrinsic extensors or flexors of the human fingers while, simultaneously, the length of other heads increases or remains constant. This implies changes of the relative position of muscle heads and adjacent tissues. Recently, relative movements of muscle heads of human EDL were reported using ultrasonography (Kawakami et al. 2004). There are two consequences of changes of muscle relative position predisposing pain within the forearm muscles:

1. *Local high strains and stresses at the interface between muscle bellies*. If a single muscle–tendon complex is lengthened, shearing of the interface between the corresponding muscle belly and adjacent tissues is highest near the location at which length changes are imposed and gradually decreases to the opposite site (for a schematic illustration see Maas et al. 2004). Thus very local differences in shear strain are expected and, if equal shear stiffness of the connective tissues between a muscle head and adjacent tissues is assumed, local differences in shear stress. Accordingly, for small distal length changes of a single head of a multi-tendoned muscle, high shear strain and stress at the muscle–belly interface is expected near the distal tendons.
2. *Co-contraction of antagonists*. Due to myofascial force transmission between a single head of multi-tendoned muscle and adjacent tissues, forces exerted at the distal tendons of muscle heads other than the target one may be affected also. If the antagonist forces remain constant, altered agonist or synergist force would lead to joint movements of the corresponding digits (i.e. finger interdependence). To prevent any undesired digit movement, co-contraction of antagonists is needed. In an experiment with monkeys that were instructed to move a single digit, co-contraction in the extrinsic flexors and extensors was reported (Schieber 1995).

Computer-related tasks, such as typing on a keyboard, require prolonged repetitive movements of fingers relative to each other. For the short-term, this may lead to very local damage of connective tissues as well as of muscle fibers (Maas 2003) and, consequently, muscle pain. For the long-term, this may result in local adaptation of connective tissues: an increased stiffness (Jaspers et al. 2002). Stiffer connective tissue at the interface between a muscle head and adjacent tissues will enhance the magnitude of force transmitted via myofascial pathways. As a consequence, the interdependence of digits is increased. To move a single digit without movements of adjacent digits co-contraction of antagonists needs to be intensified. Such events may create a downward spiral, which may ultimately result in cramp and pain in the muscles of the forearm.

It should be noted that in the present experiment a multi-tendoned rat muscle of lower hind limb was studied. For implications of myofascial force transmission on the development of muscle pain in the human forearm, species-related differences as well as differences between lower hind limb and fore limb musculature should be considered. Studies comparing rat EDL muscle to human extensor digitorum communis muscle (EDC) cannot be found in the literature. Although, striking similarities were found between cat EDL and human EDC with regard to anatomy and function (Fritz and Schmidt 1992). Furthermore, myofascial force transmission has also been shown to affect muscle properties in the forearm of humans (Kreulen et al. 2003; Smeulders et al. 2003).

In the present study, movements of a finger were simulated by 2 mm sinusoidal shortening of EDL III. Such a length change corresponds to 4% of EDL length. During typing on a keyboard, the length of the human EDC changes by only 0.70–0.74% (B.R. Jensen, personal communication). Thus, the relative length changes imposed on EDL III in the present study are higher compared to length changes of EDC during keyboard typing. However, during finger flexion from a neutral position to 90°, the length of the human EDC changes by 3.2–5.5% of whole muscle–tendon complex length (personal communication, B.R. Jensen). This indicates that the relative length changes imposed on rat EDL III

are mimicking the physiological length range that may occur in human EDC.

Concluding remarks

In the present experiment, tendon forces were measured while all four EDL muscle bellies as well as TA and EHL muscles were excited maximally. For most movements in vivo, muscles are submaximally activated. It may be argued that the stiffness of intra-, inter- and extramuscular connective tissues in the present study was higher than if muscles are not active. On the other hand, we have evidence that at lower firing frequencies myofascial force transmission becomes relatively more important (Meijer, Baan and Huijing, unpublished observations). In any case it shows that effects of myofascial force transmission during in vivo activation patterns may differ depending on the conditions. Therefore, effects of length changes of a single head that is surrounded by passive or submaximal activated muscle fibers also needs further investigation.

In conclusion, myofascial force transmission is a significant mechanism during dynamic muscle activity. The present work shows that effects of such force transmission are substantial during active shortening of a single head of multi-tendoned muscle. As multi-tendoned muscles of the forearm contribute to finger flexion and extension, these insights improve understanding of finger interdependence, as well as allowing the formulation of new hypotheses regarding the pathogenesis of repetitive strain injury within the forearm.

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References

Armstrong TJ, Buckle P, Fine LJ, Hagberg M, Jonsson B, Kilbom A, Kuorinka IA, Silverstein BA, Sjogaard G, Viikari-Juntura ER (1993) A conceptual model for work-related neck and upper-limb musculoskeletal disorders. Scand J Work Environ Health 19:73–84

Balice-Gordon RJ, Thompson WJ (1988) The organization and development of compartmentalized innervation in rat extensor digitorum longus muscle. J Physiol 398:211–231

Ettema GJC, Huijing PA (1989) Properties of the tendinous structures and series elastic component of EDL muscle-tendon complex of the rat. J Biomech 22:1209–1215

Forde MS, Punnett L, Wegman DH (2002) Pathomechanisms of work-related musculoskeletal disorders: conceptual issues. Ergonomics 45:619–630

Fritz N, Schmidt C (1992) Contractile properties of single motor units in two multi-tendoned muscles of the cat distal forelimb. Exp Brain Res 88:401–410

Hill AV (1938) The heat of shortening and the dynamic constants of muscle. Proc Roy Soc (Lond) B 126:136–195

Huijing PA, Baan GC (2001a) Extramuscular myofascial force transmission within the rat anterior tibial compartment: proximo-distal differences in muscle force. Acta Physiol Scand 173:297–311

Huijing PA, Baan GC (2001b) Myofascial force transmission causes interaction between adjacent muscles and connective tissue: effects of blunt dissection and compartmental fasciotomy on length force characteristics of rat extensor digitorum longus muscle. Arch Physiol Biochem 109:97–109

Huijing PA, Baan GC (2003) Myofascial force transmission: muscle relative position and length determine agonist and synergist muscle force. J Appl Physiol 94:1092–1107

Huijing PA, Baan GC, Rebel GT (1998) Non-myotendinous force transmission in rat extensor digitorum longus muscle. J Exp Biol 201:683–691

Jaspers RT, Brunner R, Baan GC, Huijing PA (2002) Acute effects of intramuscular aponeurotomy and tenotomy on multitendoned rat EDL: indications for local adaptation of intramuscular connective tissue. Anat Rec 266:123–135

Kawakami Y, Huijing PA, Ito M, Muraoka Y, Kubo K, Fukunaga T (2004). In vivo myofascial force transmission between passive EDL muscle segments in humans. 14th Biennal Meeting of the European Society of Biomechanics, The Netherlands

Kreulen M, Smeulders MJC, Hage JJ, Huijing PA (2003) Biomechanical aspects of progressive flexor carpi ulnaris muscle dissection. J Bone Joint Surg [Br] 85:856–859

Maas H (2003) Myofascial force transmission: intra-, inter- and extramuscular pathways. Faculty of Human Movement Sciences. Vrije Universiteit, Amsterdam

Maas H, Baan GC, Huijing PA (2001) Intermuscular interaction via myofascial force transmission: effects of tibialis anterior and extensor hallucis longus length on force transmission from rat extensor digitorum longus muscle. J Biomech 34:927–940

Maas H, Jaspers RT, Baan GC, Huijing PA (2003a) Myofascial force transmission between a single muscle head and adjacent tissues: length effects of head III of rat EDL. J Appl Physiol 95:2004–2013

Maas H, Yucesoy CA, Baan GC, Huijing PA (2003b) Implications of muscle relative position as a co-determinant of isometric muscle force: a review and some experimental results. J Mech Med Biol 3:145–168

Maas H, Baan GC, Huijing PA, Yucesoy CA, Koopman BH, Grootenboer HJ (2003c) The relative position of EDL muscle affects the length of sarcomeres within muscle fibers: experimental results and finite element modeling. J Biomech Eng 125:745–753

Maas H, Baan GC, Huijing PA (2004) Muscle force is determined also by muscle relative position: isolated effects. J Biomech 37:99–110

Sandercock TG (2000) Nonlinear summation of force in cat soleus muscle results primarily from stretch of the common-elastic elements. J Appl Physiol 89:2206–2214

Schieber MH (1995) Muscular production of individuated finger movements: the roles of extrinsic finger muscles. J Neurosci 15:284–297

Smeulders MJC, Kreulen M, Huijing PA (2003) Inter- and extramuscular connections determine muscle properties in spastic patients by myofascial force transmission. International Society of Biomechanics XIXth Congress, Dunedin, New Zealand, University of Otago

Visser B, Dieën JHv (2004) Pathophysiology of work related upper extremity muscle disorders. J Electromyogr Kinesiol (in press)

Willems ME, Stauber WT (1999) Isometric and concentric performance of electrically stimulated ankle plantar flexor muscles in intact rat. Exp Physiol 84:379–389

Woittiez RD, Brand C, de Haan A, Hollander AP, Huijing PA, van der Tak R, Rijnsburger WH (1987) A multipurpose muscle ergometer. J Biomech 20: 215–218